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A WEST AMERICAN JOURNAL OF BOTANY

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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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DEVELOPMENT OF THE FEMALE GAMETOPHYTE IN ERYTHRONIUM HELENAE AND ERYTHRONIUM TUOLUMNENSE

Marion S. Cave

The type of development of the female gametophyte which Bambacioni (2) described for *Fritillaria* in 1928 has been shown to occur in the first five of the ten genera listed by Hutchinson (10) in the tribe Tulipeae: *Erythronium, Fritillaria, Tulipa, Gagea, Lilium, Lloydia, Nomocharis, Notholirion, Giraldiella,* and *Calochortus.* In this type of development, of the four nuclei resulting from the two divisions of meiosis, three migrate to the chalazal end of the embryo sac while the fourth remains at the micropylar end. At the following division the latter divides normally giving rise to two haploid nuclei. The chromosomes of the three dividing chalazal nuclei become aligned on one spindle, thus giving rise to two daughter nuclei, each of which has 3n chromosomes. This second group of four nuclei goes through the final division to produce an eight-nucleate gametophyte with four haploid nuclei at the micropylar end and four triploid at the chalazal. The primary endosperm nucleus is formed by fusion of a polar nucleus from each group and is thus 4n.

Representatives of the five genera in which the *Fritillaria* type of female gametophyte development is known are: *Fritillaria persica* (2); *Tulipa Gesneriana* (3), and a triploid form of the same (4); *Erythronium Dens-canis* (9), and *E. japonicum* (13); *Lilium Henryi* (6), *L. philippinense* (15), *L. tigrinum* (20), and *Cardiocrinum cordatum* Makino (= *Lilium cordifolium* Thunberg) (12); *Gagea minima* and *G. lutea* (11, 19), *G. ova, G. graminifolia* and *G. tenera* (14).

So far as the author knows no work has yet been published on *Lloydia, Giraldiella, Notholirion* and *Nomocharis. Calochortus* (5) is the only genus of the tribe thus far shown to have the "normal" type of macrosporogenesis and development of the female gametophyte.

In *Erythronium* both the *Fritillaria* and *Adoxa* types of development have been described. Hrubý (9) described the process in *Erythronium Dens-canis* with twelve pairs of chromosomes up to the stage where three nuclei are seen at the chalazal end and it may be assumed that this species would hold to the *Fritillaria* type. Oikawa (13) has followed the complete development in *Erythronium japonicum* (n = 12) and found it to be of the *Fritillaria* type. However, Cooper (7) has found the *Adoxa* type in a 22-paired *Erythronium albidum.* Schaffner (17) described gametophyte development for *Erythronium americanum* and *E. albidum* (both with twelve pairs of chromosomes). From his description and figures development seems to follow the *Adoxa* scheme, but

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Madroño, Vol. 6, pp. 177–208. April 17, 1942.

since this work was done prior to 1928 there may be a possibility that Schaffner missed seeing the chalazal fusion as did all other workers before this time. Guerin (8) stated that the development in *Erythronium Dens-canis* is analagous to that which has been known "depuis longtemps chez *Lilium, Tulipa,* et *Fritillaria.*"

According to Applegate (1) there are three to four species of *Erythronium* in Eurasia, five in North America east of the Rockies, and fifteen west of the Rockies. Since those of eastern North America and Europe and Asia apparently show differences in the type of development of the female gametophyte, it was thought that study of this point in some of the western North American species would be of interest. Investigation of two Californian species, *Erythronium helenae* Applegate of section Concolorae and *E. tuolumnense* Applegate of section Pardalinae was therefore undertaken.

MATERIALS. Ovaries of these two species of *Erythronium* were fixed in CRAF, dehydrated by normal butyl alcohol, and embedded in paraffin. Sections were cut at 10, 15, and 20 microns. Three stains were employed: Heidenhain's iron alum haematoxylin, Stockwell's modification of Fleming's triple stain, and the Feulgen stain, counterstained with fast green. Haematoxylin was perhaps the best for sections at 10 microns but the Feulgen and fast green was by far the best for thicker sections.

DEVELOPMENT OF THE FEMALE GAMETOPHYTE

The embryo sac mother cell (the archesporial cell) is located directly below a single layer of nucellus cells (pl. 20, figs. 1 and 2). The cytoplasm is finely vacuolate throughout with a somewhat denser layer around the spindle. At metaphase of the heterotypic division (pl. 20, fig. 3) it was impossible to determine the exact number of bivalents since all metaphase plates seen were in more than one section and some of the bivalents may have been cut. However, there seemed to be around twelve in *E. helenae.* No heterotypic mitoses were observed in *E. tuolumnense,* but somatic plates indicated no large number such as Cooper (7) found in *E. albidum.*

The two nuclei resulting from the heterotypic division lie at opposite ends of the embryo sac (pl. 21, fig. 4). There is no resting period at this time and the homeotypic division proceeds at once. The spindles of this division also are surrounded by a dense layer of cytoplasm (pl. 21, figs. 5 and 6). No vacuole is yet observable in the sac.

At the end of this division there are four haploid nuclei in the sac. In *Erythronium helenae,* but not in *E. tuolumnense,* faint lines which are apparently fibers are often seen connecting the nuclei. Text figure 1 which is a camera lucida drawing of figure 8 (pl. 22) shows that fibers connect the two central nuclei not only with each other but also with the nuclei at the micropylar and chalazal ends. Stenar's (18) figures 3b and 7c show connecting fibers in

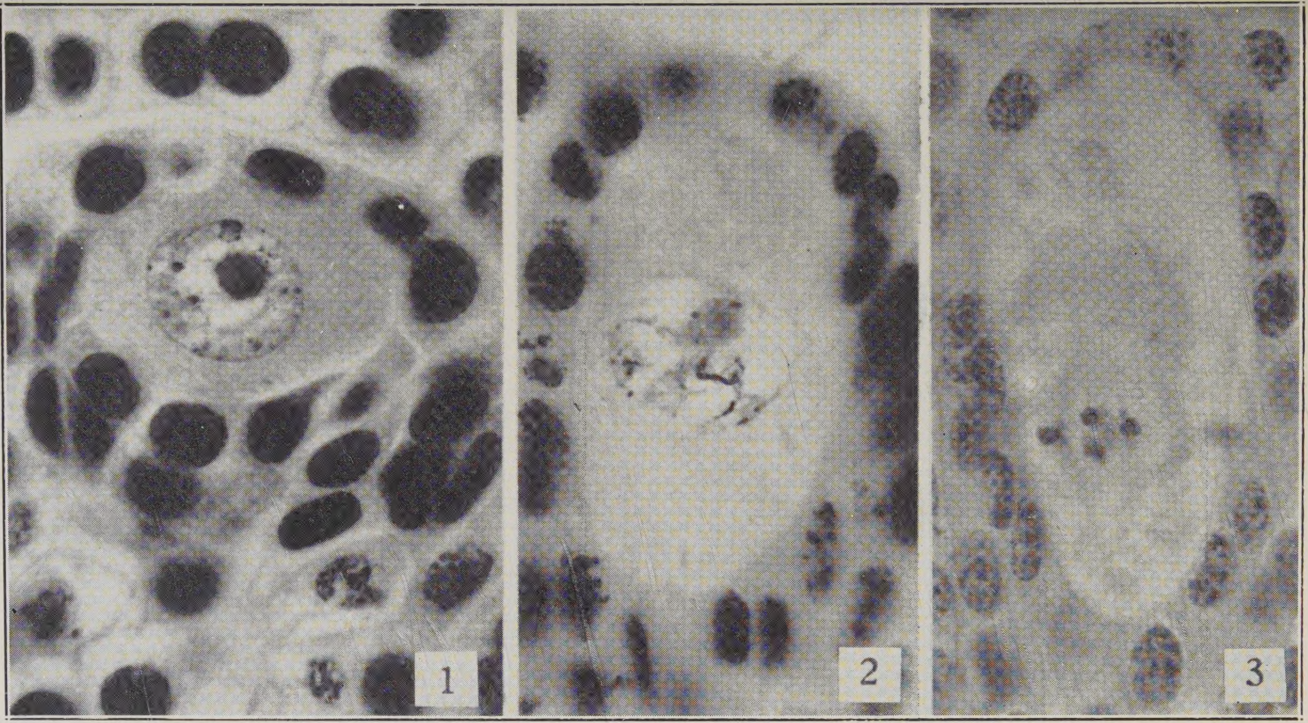

PLATE 20. DEVELOPMENT OF FEMALE GAMETOPHYTE IN ERYTHRONIUM. Fig. 1. Archesporial or embryo sac mother cell in *E. helenae.* Fig. 2. Prophase of heterotypic division in *E. tuolumnense.* Fig. 3. Metaphase of heterotypic division in *E. helenae.* All × 700.

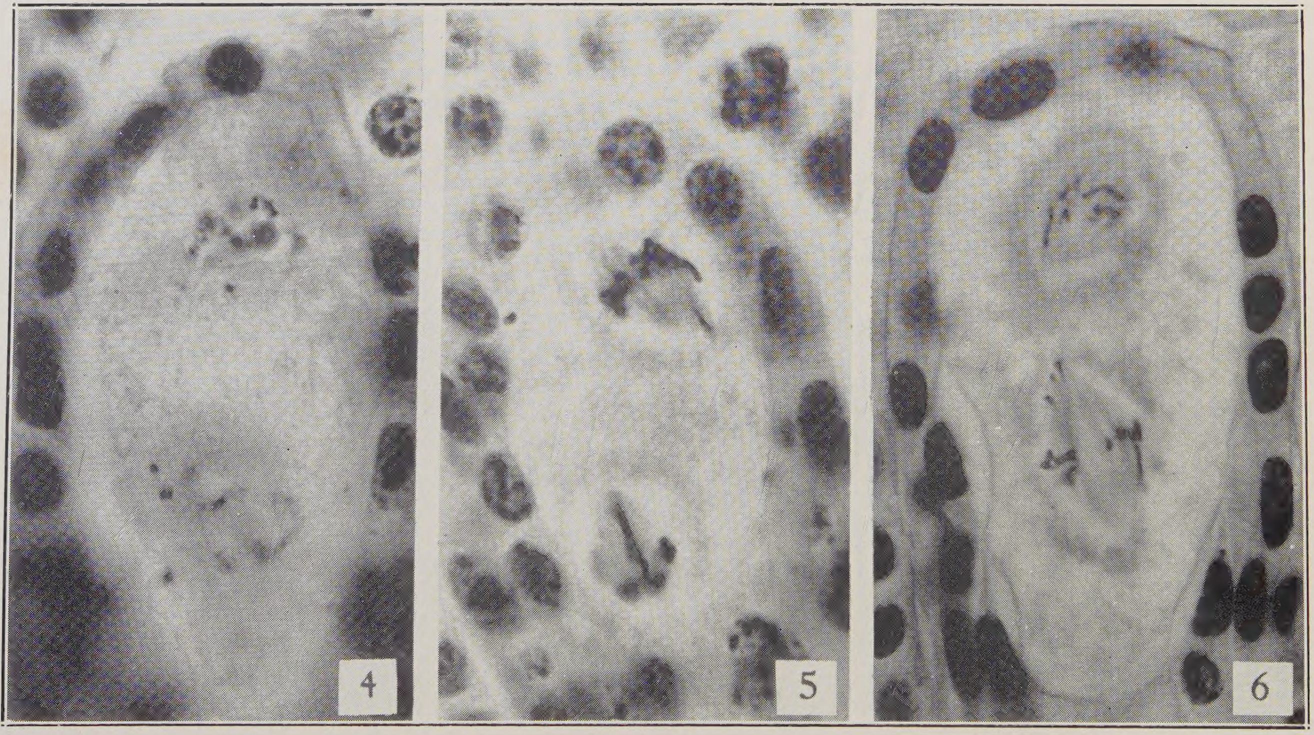

Plate 21. Development of female gametophyte in Erythronium. Fig. 4. Two nuclei resulting from heterotypic division in *E. helenae*. Fig. 5. Prophase of second division in *E. tuolumnense*. Fig. 6. Prophase of second division in *E. helenae*. Note dense cytoplasmic region around spindles. All × 700.

Gagea lutea and *G. minima* in the same configuration. Figure 7 (pl. 22) shows three nuclei at the micropylar end connected by fibers and the lowest of these furthermore connected with the nucleus at the chalazal end (in the adjacent section). Bambacioni and Giombini's (3) figure 9 in *Tulipa Gesneriana* shows a similar arrangement of fibers. In Romanov's (14) photomicrographs of *Gagea graminifolia* in his figure 7c the three chalazal nuclei can be seen connected by faint fibers. Joshi (11) mentions secondary spindle fibers arising to connect the homeotypic spindles in *Gagea fascicularis.*

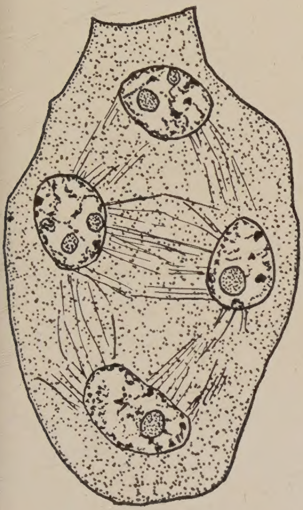

FIG. 1. Four haploid nuclei in *Erythronium helenae* all connected by fibers (camera lucida drawing of embryo sac shown in pl. 22, fig. 8).

Since these four haploid nuclei are the result of meiosis and therefore correspond to the four macrospores of a "normal" macrosporogenesis which are separated by cell walls, it may be that the fibers under discussion represent vestigial traces of cell wall initiation between the spores. If walls should form across all the fibers in figures 7 and 8 (pl. 22) each nucleus would then be separated from every other as in spore formation. A somewhat similar condition exists in a young multicellular endosperm where fibers arise to connect all the nuclei, and walls separating them then appear across the fibers throughout the endosperm. However, no walls are produced between the haploid nuclei in the embryo sac and the fibers have completely disappeared by the beginning of third prophase.

In both species three of the four haploid nuclei migrate to the chalazal end of the sac. In *E. tuolumnense* a large vacuole separates the three chalazal nuclei from the micropylar and a smaller vacuole is found at the center of the three (pl. 22, fig. 9). In *E. helenae* no vacuole is present until the second four-nucleate stage (pl. 23, fig. 12 and pl. 24, fig. 14).

At prophase of the third division the three chalazal nuclei start to fuse (pl. 23, figs. 10 and 11). Often from telophase of the second division through metaphase and telophase of the third in *E. helenae* many small bodies in the cytoplasm which stain black with haematoxylin, but do not stain with the Feulgen technique, are seen (pl. 23, fig. 12). They are pictured by Schaffner (17) in *E. albidum* in his figure 59 although this is apparently only the telophase of the first division. Hrubý shows them at the telophase of the second division and suggests that they are leucoplasts since they stain faint blue with picroindigocarmine. The writer has seen them also at the third division in *Lilium longiflorum* and Sargant (16) shows them in *Lilium Martagon*. They were also noted by Stenar (18) in *Gagea lutea*.

In the third division it is apparent that there are many more chromosomes in the mitosis at the chalazal end than in that at the micropylar (pl. 23, fig. 12 and pl. 24, fig. 13). Figure 13 (pl. 24) is a polar view of the chalazal nucleus at anaphase of the third division. All the chromosomes are not in focus but many more than the haploid number seem to be present.

In both species the second four-nucleate stage is characterized by two large elongated nuclei at the chalazal end separated by a vacuole from the two more nearly spherical nuclei at the micropylar end (pl. 24, fig. 14). A fourth division occurs to give rise to an eight-nucleate female gametophyte (pl. 24, fig. 15). The inner chalazal nucleus divides into two nuclei by means of a more or less abortive mitosis (pl. 24, fig. 15). In flowers which had been open several days fusion of the polar nuclei had not yet taken place.

SUMMARY

1. A study was made of the female gametophyte of two Californian species of *Erythronium, E. helenae* Applegate and *E. tuolumnense* Applegate, with a view to comparing their development with that found in eastern North American and Eurasian species.

2. Three of the four haploid nuclei resulting from meiosis migrate to the chalazal end of the embryo sac while the fourth goes to the micropylar end. In the following division the micropylar nucleus divides normally giving rise to two haploid nuclei, whereas the chromosomes of the three chalazal nuclei become aligned on one spindle and produce two 3n daughter nuclei. Each of the four nuclei now found in the embryo sac divides normally once again to give rise to an eight-nucleate gametophyte with three haploid nuclei at the micropylar end, three triploid at the chalazal, and one haploid and one triploid polar nucleus in the center.

3. In the two Californian species of *Erythronium* investigated development of the female gametophyte therefore follows the *Fritillaria* scheme as is true for the Eurasian species, while the *Adoxa* scheme occurs in *Erythronium albidum* from eastern North America.

Department of Botany,
University of California, Berkeley,
September 5, 1941.

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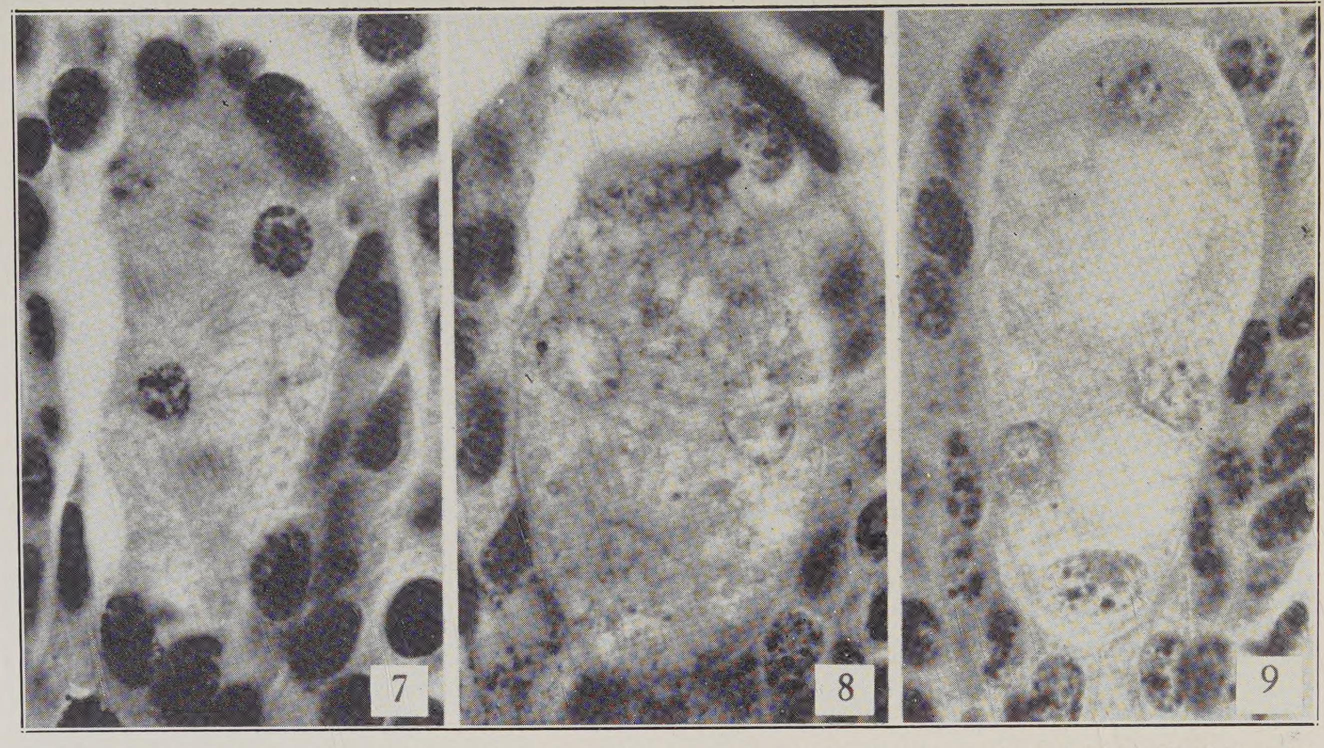

PLATE 22. DEVELOPMENT OF FEMALE GAMETOPHYTE IN ERYTHRONIUM. Fig. 7. *E. helenae:* three of the four haploid nuclei connected by fibers; the chalazal nucleus is in the adjacent section but connecting fibers can be seen. Fig. 8. Four haploid nuclei in *E. helenae* all connected by fibers, some of which are out of focus (see text fig. 1). Fig. 9. Four haploid nuclei of *E. tuolumnense* separated by vacuoles. All × 700.

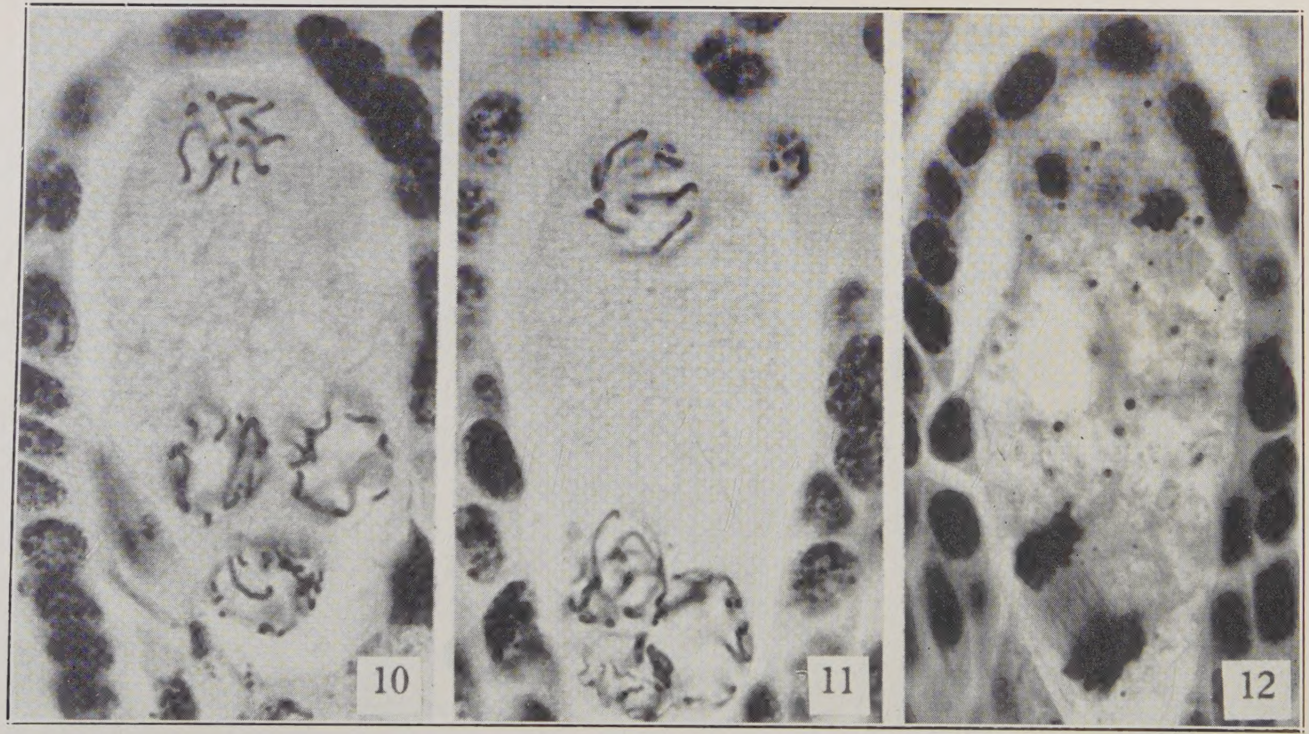

Plate 23. Development of female gametophyte in Erythronium. Fig. 10. Third prophase in *E. helenae*. Fig. 11. Slightly later than Fig. 10; chromosomes of chalazal nuclei becoming aligned on one spindle. Fig. 12. Third telophase in *E. helenae:* note dark bodies and larger chromatin masses at chalazal end. All ×700.

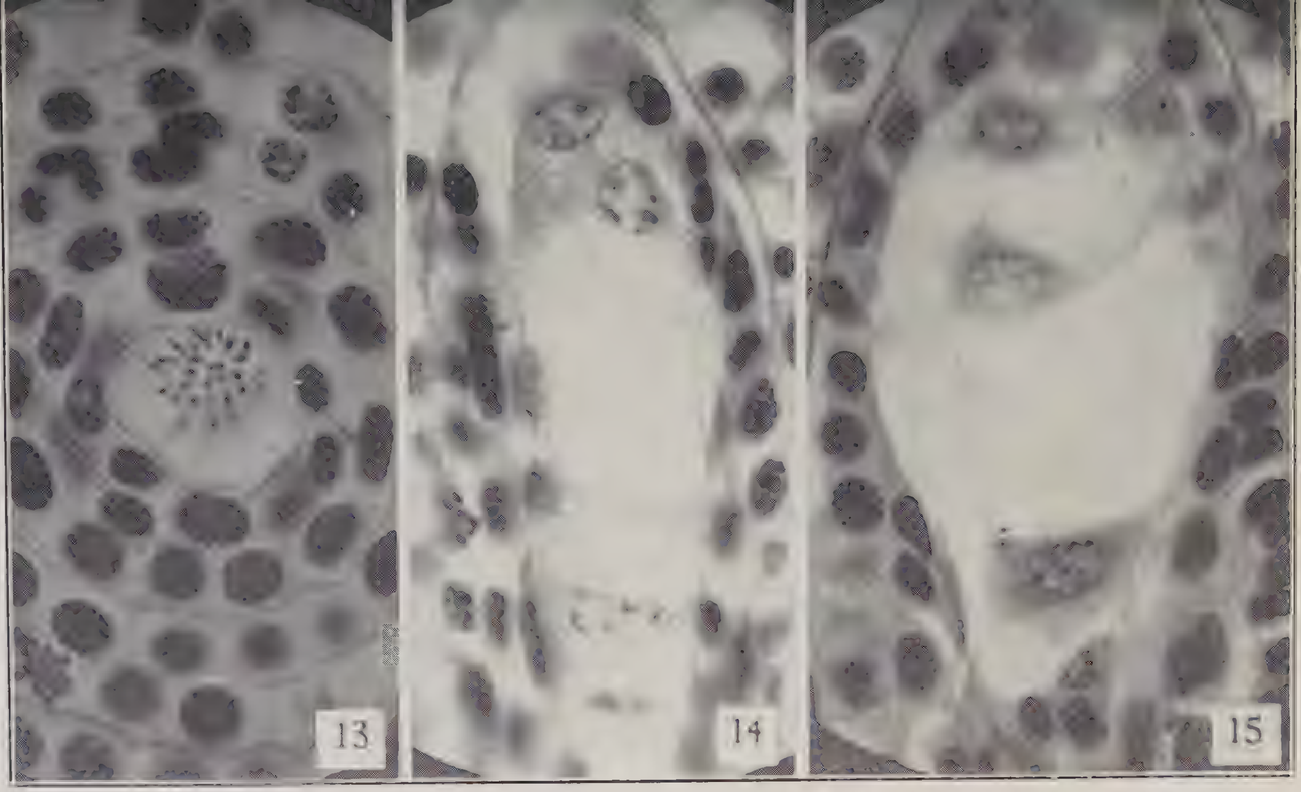

PLATE 24. DEVELOPMENT OF FEMALE GAMETOPHYTE IN ERYTHRONIUM. Fig. 13. Polar view of third anaphase in *E. helenae*. Fig. 14. Second four-nucleate stage in *E. helenae*. Fig. 15. Eight-nucleate female gametophyte of *E. helenae*. All × 500.

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SOME CHEMICAL PROPERTIES OF EUCALYPTUS IN RELATION TO THEIR EVOLUTIONARY STATUS

James B. McNair

This paper presents comparisons of morphological and chemical characteristics of members of the genus *Eucalyptus* and shows that primitive species are primitive both morphologically and chemically and more recent species are advanced both morphologically and chemically. Chemical advance involves oxidation. But chemical and morphological advances do not necessarily progress hand-in-hand.

Baker and Smith (1, 2) after thirty years work classified the genus chemically and phylogenetically. Their phylogenetic ar-

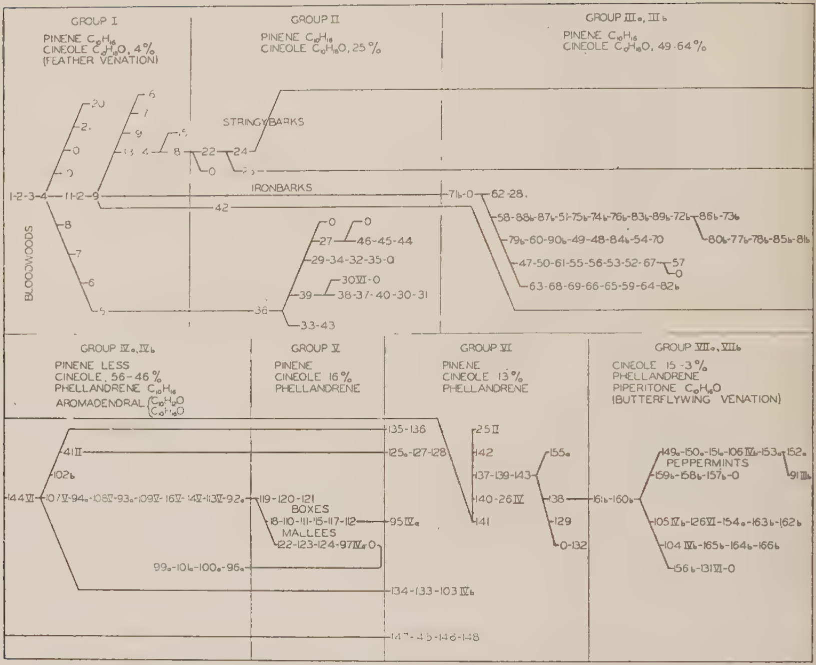

Fig. 1. Phylogenetic tree of *Eucalyptus* species portraying both systematic and chemical relationships.

rangement is shown in figure 1 and their seven chemical groups are given in Table 1. If we consider the groups of Baker and Smith in relation to the phylogenetic tree made by them it is apparent that each group represents a horizontal cross section of their phylogenetic tree (fig. 1) and consequently sometimes includes heterogeneous species which are products of different branches of descent (not natural groups or genetic sequences) and sometimes includes reversions. In other words each Baker and Smith group represents a stratum or phase in the evolutionary development of the genus. So we find (fig. 1) that group II includes three separate natural sequences, 22. *E. Wilkinsonia,* 23. *E. eugenioides,* and 24. *E. umbra* all descendants of 18. *E. nigra;* 42. *E. peniculata* from 9. *E. botryoides;* and 36. *E. maculata* and its numerous following from *E. terminalis.* Group VI has five separate systematic series and in groups IVa and IVb are found examples of natural sequences on a morphological basis which include a variety of interspersed chemical groups. For example 144. *E. obliqua* of group VI chemically is followed morphologically by 107. *E. tereticornis* of group V chemically, followed by 94. *E. tereticornis* var. *cineolofera* of group IV class (a) chemically, etc.

Consequently it is apparent from figure 1 that these plants may sometimes combine advanced systematic characters with more primitive chemical characteristics, for example, 105 IVb which is chemically in group IV but morphologically in group VII. In still other cases primitive morphological characters seem to have been retained by plants in chemically advanced positions, for example, 114 V between 116 V and 113 V. It may be concluded, therefore, that the development of chemical characteristics and morphological characters do not necessarily proceed hand-in-hand; one may proceed more rapidly or less rapidly than the other. An excellent example of this is seen in the case of *E. dives, E. radiata* and *E. micrantha.*

Eucalyptus dives, the common broad leaf peppermint, occurs in Australia over vast areas and the oil from the leaves has become of importance owing to the occurrence in it of from 40 to 50 per cent of the ketone piperitone, a commercial source of thymol and menthol. With the increased economic demand it was found that certain oils said to be obtained from the leaves of *E. dives* only yielded 5 to 20 per cent of the ketone. These were at first regarded as adulterated. It was, however, shown that they were genuine oils and that *E. dives* existed in at least four varieties which were morphologically absolutely indistinguishable both in the field or in the herbarium. At first sight this difference might be expected to be due to soil or climatic conditions but this is not the case, since the different varieties may grow side by side in the field and breed true when grown in pots (7, 8, 9, 10). The young seedlings from all four kinds were morphologically identical, yet when tiny fragments of the leaves, even from plants only one and one-half inches in height were rubbed between the fingers the characteristic odor of each particular kind was readily detected.

As a result of investigations by Penfold and Morrison (11, 12, 13) extending over a period of ten years it has been found possible to separate morphologically identical trees of *E. dives, E. radiata* and *E. micrantha* into groups as a result of hybridization based upon the chemical composition of the volatile oils.

INTERRELATIONSHIPS BETWEEN PRINCIPAL CONSTITUENTS

The principle constituents of *Eucalyptus* oils are the two terpenes, pinene and phellandrene, the oxide cineole, the group of aldehydes and a ketone known collectively as aromadendral and the ketone piperitone.

PINENE. The pinene occurring in *Eucalyptus* oils is alpha pinene and it is found in two forms, one which deflects a ray of polarized light to the right (dextro) and the other which deflects to the left (laevo).

PHELLANDRENE. This terpene is somewhat extensively distributed in the oils of certain groups of *Eucalypti.* It is more pronounced in those belonging to the more recent end of the genus, and it occurs more abundantly in those species common to the

TABLE 1. AMOUNTS OF PRINCIPAL SUBSTANCES AND PHYSICAL AND CHEMICAL PROPERTIES OF EUCALYPTUS OIL GROUPS (AUSTRALIAN AND TASMANIAN)

	Group No.	Pinene $C_{10}H_{16}$	Cineole $C_{10}H_{18}O$ percentage	Phellandrene $C_{10}H_{16}$	Aromadendral Cuminal $C_{10}H_{12}O$ Cryptal $C_{10}H_{16}O$	Piperitone $C_{10}H_{16}O$	Refractive index 20° C.	Specific gravity 15° C.	Optical activity	Solubility in parts 70–80 per cent alcohol, average
Large Group No. 1	I	large	rare aver. 4.2	absent	....	....	1.4755	0.8863	+13.4	7.8
	II	large	40 – aver. 25	absent	absent	....	1.4705	.9015	+ 5.56	3.6
	III(a)	large	40–50 aver. 49	absent	rare	....	1.4670	.9159	+ 6.1	2.3
	III(b)	large	55 + aver. 64	absent	absent	....	1.4656	.9178	+ 4.28	1.4
Large Group No. 2	IV(a)	diminishing	40 + aver. 56	absent	present	....	1.4677	.9179	+ 0.5	2.6
	IV(b)	....	40 + aver. 46	present	....	....	1.4682	.9119	– 4.5	
	V	present	40 – aver. 16	rare	present	....	1.4800	.9056	– 4.0	2.3
	VI	present	40 – aver. 13	present	....	....	1.4845	.9054	– 7.0	2.1
	VII(a)	....	40 – aver. 15	large	....	present	1.4793	.8863	–32.7	2.0
	VII(b)	....	rare aver. 3	present	....	present	1.4838	.8803	–38.8	

eastern and southeastern portion of the continent of Australia and Tasmania.

CINEOLE. The constitution of cineole is probably that of cinyl oxide, $C_{10}H_{18}O$. It has been described under the names eucalyptol (its most common commercial name) and cajuputol.

When terpin is dehydrated cineole is produced. Cineole is an internal ether produced by the elimination of water between the two hydroxyl groups in terpin. Although we have no direct evidence as to the mechanism of the formation of cineole in plants, its very frequent occurrence in oils containing α-terpinene can be accounted for readily if it be assumed to be formed from either α-pinene or α-terpineol, when terpin may be regarded as an intermediate product (16, 382).

The oils from the group of *Eucalypti* known as "gums" usually contain a fairly large amount of cineole, together with pinene, and in the case of many members belonging to this group, the cineole increases in amount when the oils are stored. This increase in cineole through possible oxidation during storage apparently confirms the fact that cineole is an oxidation product of pinene.

AROMADENDRAL. The term aromadendral is used to denote the presence of one or more members of a group of characteristic aldehydes and a ketone in *Eucalyptus* oils. These aldehydes include cuminaldehyde (cuminal), phellandral and cryptal; they do not seem to occur in the oils of the earlier members of the genus (the pinene yielding group), nor in those of the more recent species, particularly those in which phellandrene is the more pronounced terpene. In these latter species the characteristic constituent is the ketone piperitone.

It may also be stated as a general rule that cymene is present in either larger or smaller amount in the oils of species containing these aldehydes.

Wallach (17) has shown that the oxidation of β-phellandrene produced a glycol, which on treating with dilute H_2SO_4 gives dihydro- and tetrahydrocuminaldehydes. Molecular re-arrangement of a somewhat similar character may perhaps take place naturally.

PIPERITONE. Piperitone is the peppermint ketone of *Eucalyptus* oils. It is an unsaturated ketone $C_{10}H_{16}O$ with one double bond. It appears to occur only in the oils of species occupying the more recent end of the genus and is not found in the oil of any member of the groups occupying the anterior position, in the evolutionary sequence of the genus. In the oils of most species, piperitone is found associated with the corresponding l-rotatory secondary alcohol piperitol. Phellandrene in *Eucalyptus* oils is often associated with l-piperitone, but not always, although it may be accepted that the most pronounced phellandrene *Eucalyptus* oils always contain this ketone in smaller or larger amounts.

Hughesdon, Smith and Read (4) have directed attention to the fact that l-piperitone always occurs in nature in association with

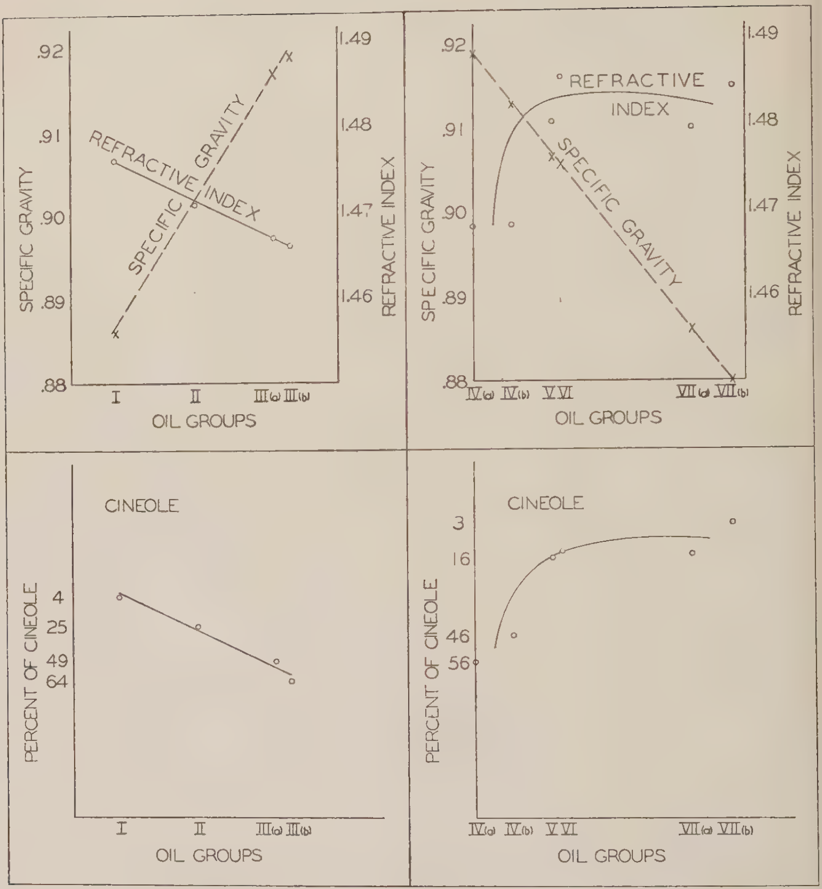

Fig. 2. Graphs showing the specific gravities, refractive indices and percentages of cineole of *Eucalyptus* oil groups.

l-α-phellandrene and l-piperitol and it is possible that some relationship exists between these substances. In the laboratory it has been found that the reduction of either d- l- or dl-piperitone with sodium in alcoholic solution yields dl-isomenthols and dl-menthols, some dl-α-phellandrene being formed simultaneously.

Comparison of Specific Gravities and Refractive Indices

Based on their specific gravities (and concomitant refractive indices) *Eucalyptus* oils may be divided into two large groups. The first and most primitive group includes groups I, II, IIIa and IIIb of Baker and Smith (2). (Table I and text fig. 2).

The second and less primitive group includes groups IVa, IVb, V, VI, VIIa and VIIb of Baker and Smith (2).

In figure 2 it so happens that a straight line will pass near all the points representing the specific gravities of groups I to IIIb inclusive and that another straight line will pass near all the points representing refractive indices. Therefore, the rule that a high specific gravity is accompanied by a low refractive index and vice versa for plant volatile oils (5) is confirmed.

It is noticeable that a straight line cannot be drawn through all of the five points representing the refractive indices of groups IV to VIIb, and that the line of closest fit is a curve. Consequently it is obvious that the mixture of substances which constitutes the volatile oils of at least some of the members of this group are different from those of the groups I to IIIb where straight lines can be drawn approximately through all the points representing the specific gravities and another straight line will lie near to all of the points representing refractive indices. Different mixtures of substances are also indicated in figure 2 by the fact that for groups I to IIIb the refractive index decreases with advance in plant evolutionary position while for groups IV to VII the reverse is true. Likewise there is a difference in the directional change in specific gravities for groups I to IIIb and IV to VII. In groups I to IIIb the specific gravity increases with advance in plant evolutionary position while in groups IV to VII the reverse takes place.

Increase in Oxygenated Bodies with Evolutionary Progress

According to the general theory for angiosperm volatile oil behavior, the specific gravity should increase and the refractive index should decrease with advance in evolution (6). The oils of groups IVa to VIIb contain principally pinene, its oxidation product cineole, and phellandrene and its oxidation products, cuminal, cryptal, phellandrol and piperitone. From Table 1 it is seen that pinene and cineole are diminishing while the other substances mentioned are increasing with progress from IVa to VIIb. The removal of a heavy substance from the oil would decrease its specific gravity. Therefore the subtraction of pinene which has a specific gravity of 0.865 at 15 degrees would not tend to decrease the specific gravity of the oil because its specific gravity is lower than that of the average specific gravity of groups IVa to VIIb (Table 1). However, if cineole be taken out the specific gravity would tend to lower because cineole with its specific gravity of 0.930 at 15 degrees is greater than the average specific gravity of the oils of the groups here considered. The content of cineole rapidly diminishes (56 per cent to 3 per cent) in these groups. The other main oxygenated bodies of these groups also have specific gravities near that of cineole. Consequently neither the amounts of these compounds nor that of cineole increases from groups IVa to VIIb enough to change the diminishing trend of the specific gravity. Should the total amount of the oxygenated bodies increase from IVa to VIIb it is obvious that the specific gravity would also increase. Consequently we may conclude that the volatile oils of *Eucalyptus* species when in their native habitat, increase in specific gravity with the increase in plant evolution *except* where the oxygenated bodies decrease in amount with the increase in evolution.

The refractive index of cineole (1.4596 at 20 degrees) is lower than the average refractive index for the group oils. Consequently its removal would tend to raise the refractive index of the group oils. Otherwise the refractive index would increase with evolutionary progress.

Table 1 shows that chemical analysis has found the number and variety of oxidation products to increase with advance in evolutionary position in the genus. Cineole, the oxidation product of pinene, is found in all of the groups. Aromadendral (which is mostly cuminal and cryptal oxidation products of phellandrene) is found in groups III, IV and V. Piperitone with which is associated phellandrol, both oxidation products of phellandrene are found in group VII.

The increase in the number and variety of oxidation products is likewise shown by the increase in the solubility of the crude oils in 80 per cent alcohol from groups IVa to VIIb (Table 1). For the oxidation products are soluble in alcohol whereas the terpenes, pinene and phellandrene are comparatively insoluble. The amount of cineole rapidly decreases from group IVa to VIIb and yet the solubility increases. Consequently some other oxidation products must replace the removed cineole.

Optical Rotation

A glance at Table 1 shows clearly that the average optical rotation becomes more laevo-rotatory as the evolutionary sequence of the groups advance. There are a number of dextro- and laevo-rotatory substances in the oils. There are present in varying amounts both dextro- and laevo-pinene and d- and l-phellandrene. There are also l-piperitone, d-terpinol and d-eudesmol. Most of the pinene is dextro- and most of the phellandrene is laevo-rotatory; d-pinene accounts for the predominant d-rotation in groups I, II, IIIa and IIIb and l-phellandrene and l-piperitone for the predominant l-rotation in the remaining groups.

Ontogeny and Phylogeny

The *Eucalypti* furnish an excellent chemical counterpart to the morphological theory of Haeckel (3) that ontogeny recapitulates phylogeny, that the organism in its development is to a great extent an epitome of the form modifications undergone by the successive ancestors of the species in the course of their historic development. Oil from the younger seedlings contains more d-pinene and less cineole (that is more hydrocarbon and less oxygenated products) than does that from the saplings two or three years old, and the maximum cineole content is reached in the oil collected from older trees (2). This is true also for the leaves which are reproduced from lopped old trees, and the oil from seven months "suckers" contains more cineole and less pinene than does that from twelve months old seedlings, while that from fifteen months old "suckers" follows the same rule in respect to two and one-half year old seedlings. The increase in the amount of cineole with progress in evolution in Large Group No. 1 of the genus is shown in Table 1.

SUMMARY

There has been orderly evolution in volatile oil characteristics of the *Eucalypti* which may be correlated with changes in morphological characteristics. However, oil groups represent cross-sections of the phylogenetic tree and not necessarily genetic sequences or natural groups of the systematist. Botanically distinct species are generally distinguished by their chemical constituents and also in some cases where morphological examination shows little or no difference, chemical analysis of the oil reveals the existence of completely distinct varieties.

With progress in evolution the amount of the hydrocarbon (terpene), pinene and its oxidation product cineole increase to a maximum, then decrease; another hydrocarbon (terpene) phellandrene and its products form a second series of compounds which is evidenced first by the appearance of aromadendral (an aldehyde and ketone mixture containing cuminaldehyde and cryptal); next phellandrene becomes a pronounced constituent and finally its ketone piperitone increases in amount.

The specific gravity increases with the increase in plant evolution, and the refractive index decreases with the increase in plant evolution, except where the oxygenated bodies decrease in amount with the increase in evolution.

The number and variety of oxidation products increase with advance in evolutionary position in the genus.

There is a tendency for the optical rotation to become more laevo-rotatory with advance in evolution caused principally by a decrease in d-pinene and an increase in l-phellandrene and its ketone l-piperitone.

Morphological and chemical phylogeny have their counterparts in ontogeny.

Los Angeles, California,
July 3, 1941.

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GRASSLAND AND RELATED VEGETATION IN NORTHERN MEXICO

Forrest Shreve

The extensive grassland area of the central United States exhibits its optimum development in Kansas and Nebraska, and extends south to the Mexican boundary only after suffering localization in occurrence and modification in character. The plains and gently falling outwash slopes of southern New Mexico and western Texas are largely occupied by a very open type of arid grassland in which *Yucca, Nolina, Dasylirion, Agave, Opuntia* and various shrubs are conspicuous. This is a transition region, in which the conditions are intermediate between the optimum ones for grassland and for desert. The vegetation is formed by an infiltration of plants from each of these vegetations, with very few dominant species that are distinctive of the transition region. In both of the states mentioned and also in southeastern Arizona there are areas of true grassland growing in favorable valleys or circling the higher mountains, and in all cases occupying relatively deep soils at elevations of 1500 to 1800 meters.

At higher elevations in northern Mexico, where climatic and soil conditions are favorable, there are some large areas of grassland. These are chiefly along the eastern base of the Sierra Madre Occidental and around the higher mountains of northern Coahuila. Grasses are also important in the transitions from grassland to encinal (evergreen oak woodland), to juniper or pinyon woodland, and to oak chaparral. Grasses are likewise important in the cactus-acacia-grassland ("cactus savanna"), which lies between the southernmost areas of desert and the grassland. In northern Chihuahua there are a number of "llanos," or grass covered plains, which are not related to the true grassland and its transitions but are distinctly a desert association occurring also in Arizona and Sonora. The aim of this paper is to describe briefly each of these types of vegetation in which grasses play a conspicuous part. Nothing will be said here in reference to the minor rôle played by grasses in the desert, their greater importance in the arid bushland which occupies the low elevations of northeastern Mexico, nor their secondary rôle in the forests of northern Mexico.

Prior to the beginning of the Madero revolution the grasslands of northern Mexico were a source of great wealth. The destruction and expropriation of most of the great cattle ranches gave the grasslands a period of over fifteen years with relatively light utilization. During the last seven years the agrarian program of the Mexican Government has brought some of the best areas of grass into cultivation. A magnificent natural sod has been destroyed in a worthy effort to help inexperienced and poorly equipped farmers to raise profitable crops of corn by dry farming methods. The recent heavy importation of foodstuffs by Mexico, for the first time in its history, is eloquent proof of the difficulties which this program has encountered.

The most extensive grasslands are in central Chihuahua, covering an area indicated on the map accompanying a paper by the writer in this journal (4). A continuous belt of varying width extends south through Durango and Zacatecas into Aguascalientes and northern Jalisco. Most of these areas are in the elevated valleys which lie between the eastern base of the Sierra Madre and the subsidiary ranges which parallel it on the east. In northern Chihuahua grassland is found in suitable situations between elevations of 1600 and approximately 2150 meters. In northern Durango there is a very gradual ascent from the central basin of the Mexican plateau to the summit of the Cuchillo de Zarca at 2000 meters. On this ascent in the region west of Mapimi the desert shrubbery is gradually replaced by grasses, and typical grassland is first met slightly below 1800 meters. In southern Durango, south of the Rio Nazas, grassland is first encountered at 1925 meters and covers a large area in the central and southern part of the state. Between Nombre de Dios, Durango, and Sombrerete, Zacatecas, broad grassland valleys rise to an elevation of 2500 meters. Similar areas also extend north from the city of Durango but are interrupted by extensive malpais areas. In the 1000 kilometers between northern Chihuahua and central Zacatecas it will be noted that there is a slight increase in the elevations between which grassland is found. In northern Coahuila the scattered belts of grassland lie between 1500 and 1800 meters.

The western face of the Sierra Madre Occidental is more precipitous than the eastern and active denudation has prevented the development of large areas suitable for domination by grasses. In northeastern Sonora there are areas and belts of grassland in localities north of Moctezuma and east of Magdalena. With decreasing altitude the transition from grass to desert is rapid. South of Moctezuma the principal display of grasses is in foothills at elevations of 450 to 900 meters, where coarse bunch grasses grow in the open stands of oak. The Sonoran grasslands are rich in species but differ in composition from the areas in Texas and Chihuahua.

On the eastern side of the Mexican plateau, along the western base of the Sierra Madre Oriental, the physical conditions differ greatly from those on the western side. The mountain axis is not so continuously elevated and has no parallel subsidiary ranges on its landward side. The highest peaks are Cerro Potosi (3800 m.) and Peñon Nevado (3664 m.). Between them, and north of the former, are gaps so low that many desert plants extend over the divide into the drainage of the Gulf of Mexico. Another important feature with reference to grassland is the prevalence of limestone along the mountain front in Coahuila and Nuevo Leon. The reluctant weathering of limestone leaves the soil shallow, the surface stony and the deep pockets of soil few. In Mexico, as in the southwestern United States, the limestone soils do not support heavy stands of grass, and desert invariably extends to much higher elevations on limestone than on other types of rock and their derived soils.

The nearest approach to areas of typical grassland on the eastern side of the plateau has been found between Mier y Noriega and Soledad, Nuevo Leon, in the lee of the Peñon Nevado range. The elevation ranges from 1700 to 2000 meters and the rainfall at a single adjacent station is 500 millimeters. On the pediments and gently rounded ridges which parallel the base of the mountains the cover is rarely more than 50 per cent grass, the remainder being other herbaceous perennials. There are frequent mottes of *Quercus cordifolia* from 5 to 6 decimeters high, as well as other shrubs and semi-succulents of greater frequency than in typical grassland.

The characteristic grasses in this region are *Bouteloua gracilis,*

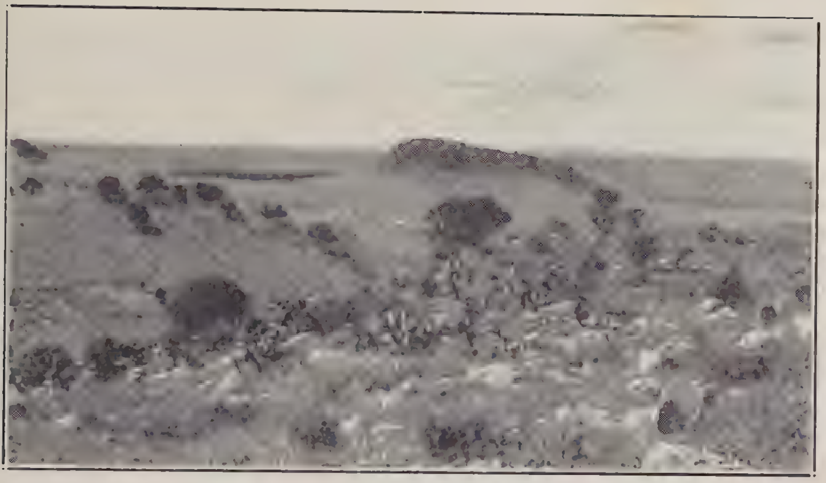

Figure 1.

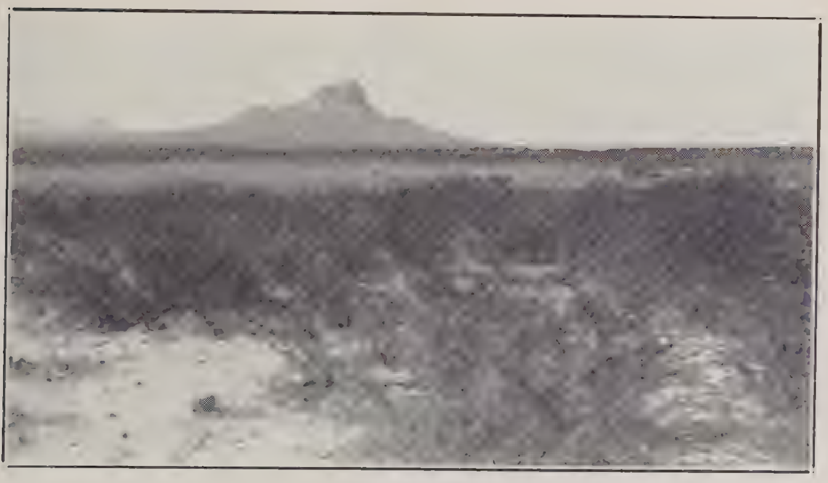

Figure 2.

Plate 25. Grassland in Northern Mexico.

Plate 25. Grassland in Northern Mexico. Fig. 1. Looking northeast across the grassland plateau of southern Durango from the lower edge of pinyon woodland in mountains near La Purisima, at 2400 meters elevation. Fig. 2. Looking across bajada with desert shrubbery of *Larrea* and *Acacia vernicosa* to small *Hilaria* llano, 65 kilometers northeast of Camargo, Chihuahua, at 1400 meters elevation.

Triodia grandiflora, Hilaria cenchroides, Lycurus phleoides, and a small slender form of *Bouteloua curtipendula.* The commonest associated plants are *Zinnia anomala, Dichondra argentea, Dyschoriste decumbens, Dyssodia setifolia, Acalypha phleoides, Florestina tripteris* and *Houstonia rubra.*

The precipitation in the Mexican grassland lies approximately between 400 and 500 millimeters on the west side of the central basin and between 500 and 600 millimeters on the east side of the mountains of northern Coahuila. The annual average for the city of Chihuahua, just below the edge of the grassland, is 385 millimeters, while for Parral, just above the grassland, it is 517 millimeters. In the city of Durango the average rainfall is 463 millimeters and at Villa Madero it is 488 millimeters, both localities being in cultivated country that was originally grassland. Charcas, San Luis Potosi, is at 2060 meters elevation on the eastern edge of the grassland, which is only locally and poorly developed there. The average annual precipitation at Charcas is 411 millimeters. Throughout the grassland areas the late winter and spring are dry and the four months, June to September, receive from 64 to 77 per cent of the annual precipitation.

The areas herein designated as grassland are occupied by "short" grasses forming a sod or turf which covers 80 per cent or more of the surface. Cacti over 20 centimeters in height, shrubs and trees are rare or absent. *Yucca, Nolina, Dasylirion* and *Hechtia* are infrequent except at the lowest altitudes and in the transition from grassland to desert. Closely associated with the grasses is a large number of herbaceous root perennials, many of which are prostrate, low, or of habit and leaf size which make them inconspicuous.

The structural and social features of the Mexican grasslands resemble those of the central United States, as described by Clements (1), Weaver and Fitzpatrick (5), Gates (2) and others. The floristic composition is similar to that of western Texas but differs materially from that of Kansas. Among the characteristic grasses of the latter state *Agropyron Smithii, Eragrostis spectabilis, Sporobolus asper, Aristida oligantha, Scheddonardus paniculatus, Stipa spartea* and *S. comata* are absent or very uncommon in Mexico. *Andropogon scoparius* is absent and *A. furcatus* is widespread but nowhere abundant. *Koeleria cristata* is abundant only at high elevations in the grassy forests.

Throughout the most extensive grass areas of Chihuahua and Durango the species of *Bouteloua* greatly dominate over the representatives of other genera. The commonest of these is *B. gracilis,* which is estimated to form at least 80 per cent of the cover in approximately 60 per cent of the grassland area. In the southern extension of the grassland, in Zacatecas and Jalisco, *Bouteloua hirsuta, B. radicosa, Hilaria cenchroides* or *Sporobolus trichodes* alternate or associate as the most common species. Throughout the grassland area large coarse grasses occur sporadically or in isolated colonies, including *Andropogon saccharoides*, *A. barbinodis*, *Stipa eminens*, *S. clandestina*, *Sporobolus airoides*, *Elyonurus tripsacoides* and *Trichloris mendocina*. Relatively moist areas are heavily carpeted by *Buchloë dactyloides*. Dry localities with shallow soil at low elevations are thickly covered with *Triodia pulchella* or well defined colonies of *Scleropogon brevifolius*. In general, however, the grasslands are as monotonous in composition as they are in their physiognomy.

The following list includes the dominant and frequently recurring grasses of the grassland areas of northern Mexico. The names are approximately in the order of abundance.

Bouteloua gracilis
Bouteloua curtipendula
Bouteloua chondrosioides
Aristida divaricata
Eragrostis mexicana
Bouteloua radicosa
Triodia pilosa
Stipa eminens
Eragrostis diffusa
Lycurus phleoides
Buchloë dactyloides
Triodia grandiflora
Andropogon saccharoides
Aristida ternipes
Eragrostis lugens
Eragrostis intermedia
Hilaria cenchroides
Muhlenbergia monticola
Stipa editorum
Triodia mutica
Scleropogon brevifolius
Sporobolus trichodes
Pappophorum Wrightii
Setaria macrostachya

Grasses which are less abundant over the entire area or only locally common are the following.

Andropogon perforatus
Aristida adscensionis
Aristida glauca
Aristida hamulosa
Bouteloua eriopoda
Bouteloua filiformis
Bouteloua hirsuta
Bouteloua Rothrockii
Elyonurus tripsacoides
Eragrostis limbata
Leptochloa dubia
Muhlenbergia polycaulis
Muhlenbergia rigida
Panicum Hallii
Panicum obtusum
Setaria geniculata
Setaria Grisebachii
Sporobolus airoides
Sporobolus Poiretii
Stipa clandestina
Stipa tenuissima
Trichloris mendocina
Triodia grandiflora
Triodia pulchella

Transition from Grassland to Encinal

At the same altitudes occupied by grassland there also occur extensive stands of encinal (evergreen oak woodland) or open stands of juniper or pinyon. These are almost invariably confined to hills and abrupt slopes or to rocky ground with shallow soil, while grassland occupies level or gently sloping areas with soil from 15 to 50 centimeters or more in depth. In open stands of woodland the floor supports a light cover of grasses which differs little in appearance and composition from pure grassland. Where the soil is rocky and irregular in depth, and the trees are abundant, a rich variety of herbaceous perennials forms more of the cover than do the grasses.

In central Chihuahua the lower edge of the encinal is often encountered at 1500 meters in very open stands of *Quercus chihuahuensis, Q. santaclarensis* or *Q. Emoryi.* In southern Durango encinal fails to find extensive areas of suitable conditions below 2150 meters, and in several districts grassland extends up to 2500 meters. In both states the texture and depth of soil appear to be the deciding conditions for the dominance of grasses or the appearance of trees. The critical season for trees is the dry period extending from February to May. Nothing is known about the comparative soil moisture of the deep soils and the rocky terrain in this region. If conditions are analogous to those investigated in Arizona the pockets and layers of the rocky soil have a higher moisture content in dry periods than the deep uniform soil has. All evergreen oaks defoliate in the early spring and simultaneously form a complete new crop of leaves. In Chihuahua in 1937, after a dry winter and delayed summer rains, the oaks were nearly leafless in July and new leaves first began to appear early in August. Even in their more favorable habitat the oaks must often be thus brought near the margin of their drought resistance. At such times they might not be able to survive on deep level soil except near streamways.

In northern Coahuila the upper edge of the grassland commonly merges into shrubbery from 1 to 2 meters in height. This vegetation forms a closed cover at slightly higher elevations and on north slopes. It so closely resembles the Pacific coast chaparral in its life forms, social aspects, and generic composition that it may well be designated by the same name. The Mexican chaparral has been described by Muller (3) as manifested on the lower western slopes of Cerro Potosi, in Nuevo Leon. The lower, open edge of the chaparral is dominated in Coahuila by shrubby oaks, notably *Quercus invaginata, Q. cordifolia, Q. Pringlei, Q. hypoxantha,* and *Q. intricata,* or else by small individuals of arborescent species. Commonly associated with the oaks, or locally outnumbering them, are *Cowania plicata, Arctostaphylos pungens, Microrhamnus ericoides, Ceanothus lanuginosus, Mimosa biuncifera, Amelanchier denticulata, Rhus microphylla, Berberis trifoliata* and *Cercocarpus mojadensis.* The prevailing limestone of northern Coahuila is not favorable to the attainment of large size by oaks and pinyons. On steep and moderate slopes the chaparral forms heavy stands and grasses are nearly absent. On level ground and gentle slopes the shrubbery is open and there is a ground cover of grasses and herbs. These circumstances bring about considerable variation in the altitude at which grassland merges into chaparral, and at which chaparral becomes dominant. The changes most commonly take place between elevations of 1500 to 1800 meters.

CACTUS-ACACIA-GRASSLAND

Along its southwestern margin the Chihuahuan Desert is bounded by a distinctive type of vegetation which lies between the desert and grassland. This is essentially a thin cover of short grass with a continuous open stand of small trees and tall platyopuntias. The striking physiognomy of this vegetation might suggest that it be designated by the loosely used term "savanna," which is often misapplied to any association of grasses and trees. True savanna is characterized by large harsh-leaved grasses of a type which rarely forms closed communities in temperate North America. The characteristic tree is *Acacia tortuosa,* which usually has a broad flat crown, and the only other tree is a much less frequent undescribed species of *Prosopis.* The platyopuntias are *Opuntia streptacantha* and *O. durangensis,* which are erect, have broad joints 30 to 40 centimeters long, and reach a height of 3 to 6 meters. The cacti usually outnumber the trees but are widely spaced or in open groups. Shrubs are very uncommon and nearly limited to *Celtis pallida* and *Acacia paucispina.* Semi-succulents are sparingly represented by *Yucca carnerosana,* which reaches a height of 5 to 12 meters. Cacti other than those mentioned are very uncommon, the one most frequently seen being the ubiquitous *Opuntia imbricata.* The representation of grasses corresponds closely with that found in the open grassland. Herbaceous perennials are more abundant in species and individuals than they are in the grassland. Many perennial herbs and several grasses grow in the cactus-acacia-grassland which are not found in the grassland. These are largely confined to the heavy shade of the tall opuntias, whereas the light shade of *Acacia,* which executes considerable movement during the day, is occupied by the prevailing sod.

It seems scarcely allowable to regard the cactus-acacia-grassland as a transition between desert and grassland. In physiognomy it carries no suggestion of either. It has most of the typical grasses of the grassland but its flora includes none of the characteristic plants of the desert except the occasional trees of *Prosopis.* Also, the three characteristic large plants are found neither in desert nor grassland.

The lower edge of the cactus-acacia-grassland is reached at about 1800 meters and its upper edge at 2000 meters, or exceptionally as high as 2200 meters. It is found only on plains, bajadas and gently rolling surfaces with soil at least 1 to 2 meters deep. The commonest type of soil is a ruddy brown clay of volcanic origin, containing from 5 to 20 per cent of well worn rock particles from 0.5 to 3 centimeters in diameter. In two localities typical stands were seen on granitic loam (near Sain Alto and near Pinos, in Zacatecas).

This type of vegetation has been observed only in southern Durango, Zacatecas, northern Jalisco and southern San Luis Potosi. It has been studied between Yerbanis and Villa Madero, Durango, between Victoria, Durango, and Rio Grande, Zacatecas, between Concepcion del Oro and Santa Maria Mañon, and near Pinos, in Zacatecas, and in the District of Lagos, Jalisco. The principal variations from the typical conditions described are east of Santa Maria Mañon, where the two opuntias form an unusually close stand, and near Arriega, San Luis Potosi, where the opuntias are dense but not more than 2 meters high, and the sod of grasses very open.

There are no available rainfall records within the range of this vegetation but the annual total can be interpolated as probably between 350 and 425 millimeters.

The most abundant herbaceous perennials of the cactus-acacia-grassland are the following.

Dichondra argentea
Evolvulus alsinoides
Alternanthera repens
Sanvitalia ocymoides
Plantago mexicana
Guilleminea densa
Spergularia mexicana
Ipomoea costellata
Drymaria arenarioides
Cyperus seslerioides
Gaura coccinea
Tetraclea Coulteri
Stevia salicifolia
Commelina scabra
Oxalis albicans
Zornia diphylla
Cassia crotalarioides
Tagetes lucida
Acalypha neomexicana
Dyschoriste decumbens
Verbena teucriifolia
Phaseolus heterophyllus
Polygala compacta
Sisyrinchium tenuifolium

Many of these plants are familiar components of the grassland as far as northern Chihuahua and western Texas, and it is noteworthy that the list includes no plants of southern range which are here near their northern limits. The grassland and its variants are here near their southern limit, and also many of their characteristic plants reach the southern end of their ranges in Jalisco.

The Hilaria Llanos

Nearly every map of Mexico indicates that the center of the northern plateau is occupied by a single extensive undrained basin, styled the "Bolson de Mapimi." As a matter of fact the area includes a large number of independent undrained basins, or bolsons, varying from a few hundred to several thousand hectares in size. Along the eastern and western edges of the plateau there are an undetermined number of bolsons which receive copious drainage waters from the slopes of the bordering mountains. The centers of these bolsons are occupied by alkaline flats and seasonal lakes. Other bolsons in the center of the plateau receive limited drainage from their surrounding hills and bajadas and are without a central playa, or lake bed. In these the floor of the bolson is nearly level and the soil is deep and fine in texture. In such situations are found the llanos, or nearly pure *Hilaria* grassland areas, which collectively cover a large expanse in northern Chihuahua. The largest are the "Llano de los Gigantes" and the "Llano de los Christianos," which are the northernmost ones that have been observed. The southernmost one that has been noted is north of Naica, in the district of Meoqui, Chihuahua. The elevation ranges from 1100 to 1300 meters.

As previously intimated the llanos are not to be regarded as part of the climatic grassland formation but rather as a desert association controlled by soil conditions. Surrounding and overlooking the llanos are invariably long outwash slopes covered with typical desert of *Larrea, Flourensia, Acacia vernicosa* and many cacti. Smaller llanos of the same character occur under very similar conditions in southern Arizona and northern Sonora, down to elevations less than 300 meters.

From 80 to 90 per cent of the cover in the llanos is formed by *Hilaria mutica,* growing continuously or in close-set tussocks. On the higher llanos there is often a small percentage of *Bouteloua gracilis* and *B. eriopoda.* There are a few very common non-gramineous associates, including *Florestina tripteris, Viguiera phenax* and *Xanthocephalum gymnospermoides.*

In addition to the regions that have been briefly described in this paper there are at least two other types of vegetation in Mexico in which grasses play a prominent part. One of these is the arid bushland of the low plains of Nuevo Leon and northern Tamaulipas, in which the open shrubbery may or may not be carpeted with annual and perennial grasses. The other is the coastal belt of Vera Cruz, with its tall coarse grass areas merging into marshes or into savanna. Neither of these vegetations has received the ecological investigation which they merit. They have little in common with the grassy areas of the highlands, either in ecological features or in floristic composition. The ecological importance of the grass family in northern Mexico may be surmised from its wealth, for in the ten states north of the Tropic of Cancer nearly five hundred species are known.

Carnegie Institution of Washington,
Desert Investigations,
Tucson, Arizona.

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CHAPARRAL

F. P. Cronemiller

Chaparral is a term commonly used in California for the dense brushfields of the Upper Sonoran life zone. This cover type is similar to the *macchie* and *garique* of the Mediterranean region and is a product of the set of climatic conditions peculiar to these areas. Its shrubby components have been termed quite accurately broad sclerophyll vegetation. The purpose of this paper is to give a chronicle of the derivation of the term "chaparral" and to encourage its use and adoption by the technician.

Chaparral evolved from *chabarra,* the Basque word for a scrub oak of the Pyrenees. The Spaniard adapted it to "a dwarf evergreen oak" and spelled it *chaparro.* He did not develop the word "chaparral," however, as he used the term "*garique*" for the cover type composed of this and species of similar growth. On his arrival in the New World he was faced with a tremendous job of inventing place names. The vast number of saints furnished an abundance of names for important places, while descriptive terms were given those of secondary importance. The convenient suffix *-al,* meaning "place of," naturally was often used. *Pinal, alisal, sausal,* designated pine groves, sycamore flats, and willow thickets. For the cover types of dense evergreen scrub oaks, *chaparral* was invented. Quickly the term came to be applied to similar cover types, and this is its usage today. Colloquially it has been applied to individual species such as one of the *Acacia* species in Mexico and to *Ceanothus cuneatus* in California. Generally the proper meaning has adhered: a place (cover type) of evergreen shrubs or dwarf trees.

In addition to chaparral the Spanish Californian used a term, *chamiso* (or *chamisal*), to designate open brush areas composed of small shrubs. The original term, *chamiza,* meant simply "kindling wood." It is not certain that he ever got entirely away from this connotation, but the vaquero used it in opposition to chaparral. To him chaparral was that kind of brush one could not ride a horse through; through *chamiso* or *chamisal,* one could. Californians have anglicized the word to "chamise" and applied it to but a single species, *Adenostoma fasiculatum.* In New Mexico, chamiso refers to *Atriplex canescens,* and in Mexico to other species and types. It would appear that the term "chamise" is hardly tenable, although widely used by the layman and some technicians.

Chaparral is without doubt a needed word; it is in general use, and is recognized by Webster and other lexicographers. The technician should not hesitate to use it.

United States Forest Service,
San Francisco, California,
February 25, 1942

NOTES ON POLEMONIACEAE

Herbert L. Mason

Gilia inconspicua Dougl. ex Hook. Bot. Mag. pl. 2883. 1829, *nomen confusum*. *Ipomopsis inconspicua* Smith, Exot. Bot. pl. 14. 1805. *Cantua parviflora* Pursh, Fl. Am. Sept. 2: 730. 1814. *Gilia parviflora* Spreng. Syst. Veg. 1: 626. 1825.

In the year 1805 J. E. Smith published in his "Exotic Botany" the name *Ipomopsis inconspicua* based upon plants cultivated in England. The plants were "raised in 1793 by Mr. Thos. Hoy, F. L. S. at Sion House, from seed brought, if I mistake not, from America. Mr. Sowerby sketched it in November of that year." Pursh, in 1814, transferred *I. inconspicua* Smith to the genus *Cantua,* renaming it *C. parviflora*. However, his doubt as to its origin in North America was expressed in the following words, "I insert this plant on the authority of Exotic Botany; but at the same time I doubt very much of its being a native of North America, and more strongly suspect it to come from Mexico." Sprengel transferred the species to *Gilia* in 1825 making the combination *G. parviflora* (Pursh) Spreng., reporting it from North America and citing *Cantua parviflora* Pursh and *Ipomopsis inconspicua* Smith as synonyms. Hooker in 1829 published a manuscript name of Douglas whereby Douglas referred *Ipomopsis inconspicua* Smith to the genus *Gilia* as *G. inconspicua* (Smith) Douglas. All three of the above mentioned names were cited as synonyms. Hooker's remarks are enlightening, "Of the authors who have hitherto described this plant, Smith alone has seen specimens which were cultivated at Sion House, in 1793, from seed which he supposed to be brought from some part of America. Pursh imagined it to be a native of America: but it was reserved for the indefatigable Mr. Douglas to determine its exact locality. He discovered it in the woodless tracts, or sandy barrens on the Southern branches of the river Columbia, on the Northwest coast of America, growing under the shade of *Purshia* (*Tigarea.* Ph.) *tridentata* and some species of *Artemisia."*

The descriptions by Smith and by Hooker are each accompanied by illustrations in color. It is obvious that the plants illustrated in each case are the same species. It is also obvious that the plants illustrated are not of a type known as yet from the interior of the Columbia River region in northwestern America. Nor does Hooker's illustration agree with the Douglas specimen in the Hooker Herbarium labeled in Hooker's handwriting *"Gilia inconspicua* Douglas." The description given by Hooker more nearly fits the plant illustrated. It would seem that the description was drawn from fresh material as was the illustration, and that an error was made in the source of the seed that gave rise to the plant. The description and the illustration of Hooker fit *Ipomopsis inconspicua* Smith, whatever that species may be.

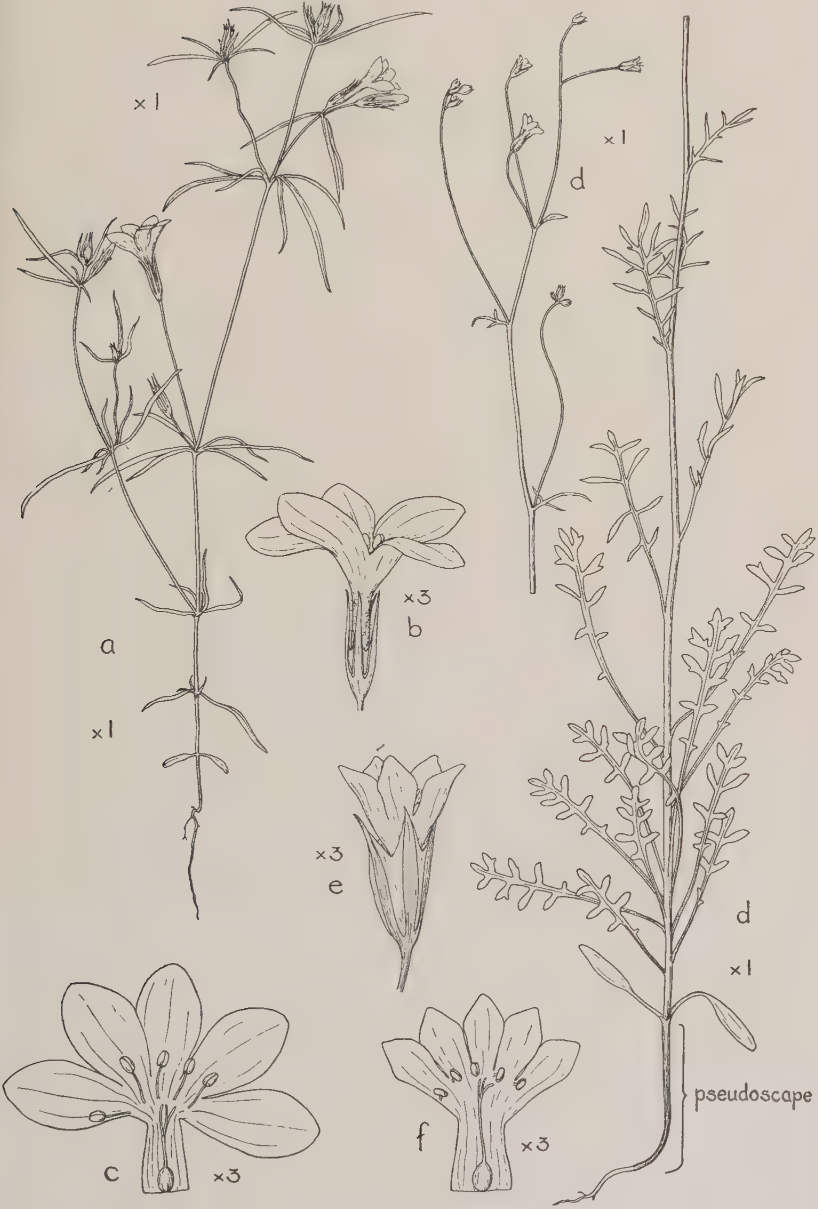

Plate 26. Linanthus Wigginsii and Gilia Clokeyi. Figs. a–c, *Linanthus Wigginsii;* figs. d–f, *Gilia Clokeyi.*

Later botanists have largely gauged their concept of *Gilia inconspicua* on the specimen of Douglas rather than on the description and illustration of either Smith or Hooker. As a result, the name *G. inconspicua* Dougl. ex Hook. is erroneously applied to the plant of the arid interior of the Great Basin of North America. Smith's plant was grown in England and described before any botanist had traversed that portion of the interior of America. The next oldest available name for this group of plants is *Gilia sinuata* Dougl. ex Benth. based on specimens collected by Douglas from near the confluence of the Okanogan River with the Columbia. This entity has been regarded by different authors as distinct either specifically or varietally from *G. inconspicua* Dougl. ex Hook. or as completely synonymous with that species. At any rate the plants represented by these names constitute an exceedingly variable genetic complex, and an eco-genetic analysis must be made before a clear understanding of the taxonomy of the group is possible.

The identity of the plants represented by the name *Ipomopsis inconspicua* Smith is not easy to determine. It seems probable that if they were derived from western North America they must have come from the coastal region. In North America plants of the group now passing under the name *Gilia multicaulis* Benth. are an excellent match for the illustrations of Smith and Hooker and could well have been collected at Monterey, San Francisco or Bodega, points visited by most of the early exploring expeditions. In both illustrations mentioned above, only portions of the plants are represented and these are not sufficiently complete to make identification certain. On the other hand, *Gilia laciniata* Benth. and *G. valdiviensis* Griseb. of South America are also close. Because of the permanent uncertainty as to the identity of Smith's original material the name *Gilia inconspicua* should be designated as a *nomen confusum.*

Gilia Clokeyi sp. nov. Herba annua erecta, 5–30 cm. alta, plerumque pseudoscapo evidente, 15–25 mm. alto; caules infra plerumque simplices in inflorescentibus ramosi; cotyledones lineari-spatulati, 12–16 mm. longi, 2–2.5 mm. lati, in petiolos graciles attenuati; folia in ambitu anguste oblonga, alterna, basi non rosulata in inflorescentibus abrupte reducta bracteata, pinnate vel bipinnate lobata, lobis aliquanto remotis, foliorum inferiorum segmentis ultimis ovatis, superiorum lanceolatis, glabra vel rarius sparse floccosa tandem glabrescentia, textura delicata; pedicelli atque ramuli florales ultimi glandulis paucis nigris capitellatis; calyx infra sinus membranaceus, membranis aliquanto distensis; corolla infundibuliformis, 6–9 mm. longa, pallido-coerulea vel fere alba, faucibus luteis, 1–1.5 mm. longis, tubo luteo, intus glabro, 3 mm. longo, lobis rhomboideis, circa 3 mm. longis; stamina in sinubus corollae affixa, antheris subsessilibus, circa 0.6 mm. longis, albis vel pallido-coeruleis, polline antheris similiter tincto;

pistillum 3–9 mm. altum, stylo apice diviso, ramis 0.5–1 mm. longis; capsula late ovoidea; semina matura non visa.

Erect annual 5–30 cm. high, usually with an evident pseudoscape 15–25 mm. high; stems usually simple below, openly branched in the inflorescence; cotyledons linear spatulate, 12–16 mm. long, 2–2.5 mm. wide, the lower one-third or one-half narrowed to a slender petiole; leaves narrowly oblong in outline, alternate, not in a basal rosette, becoming abruptly reduced and bracteate in the inflorescence, pinnately, or sometimes bipinnately lobed, the lobes somewhat remote, the ultimate segments of the lower leaves ovate, those of the upper lanceolate, glabrous, or more rarely sparingly floccose and becoming glabrate, texture thin and delicate; pedicels and ultimate branches of the inflorescence with a few black tack-shaped glands; calyx membranous below the sinuses, the membrane somewhat distended; corolla funnelform, 6–9 mm. long, pale blue to almost white, lobes rhomboid about 3 mm. long, throat and tube yellow, throat 1–1.5 mm. long, the tube 3 mm. long, glabrous within; stamens inserted in the sinuses of the corolla lobes, anthers subsessile about 0.6 mm. long, white to pale blue, pollen of the same color; pistil 3–9 mm. high, style divided at the tip, the three branches 0.5–1 mm. long; capsule broadly ovoid, mature seed not seen.

Type. Larrea belt, altitude 1200 meters, north base of limestone ledge, Red Rocks, Charleston Mountains, Clark County, Nevada, March 31, 1940, *I. W. Clokey 8599* (Clokey Herbarium at the Herbarium of the University of California). Other collections. Talus slopes above Wilson's Ranch, Charleston Mountains, Clark County, Nevada, May 3, 1939, *Bassett Maguire 16620*.

Gilia Clokeyi has been passing with a complex group of plants as *Gilia inconspicua* (Smith) Dougl., a name which, as has been indicated above, is of uncertain identity. The newly recognized entity may be distinguished readily by the lack of a rosette of congested leaves at the base of the stem, also by the essentially glabrous herbage, remotely lobed leaf blades and long narrow cotyledons.

Linanthus Wigginsii sp. nov. Herba annua, 3–12 cm. alta simplex vel pauciramosa; internodia 5–50 mm. longa, pilis densis sparsisve, debilibus brevibus contortis, tandem glabrescentibus; cotyledones lineari-spatulati, 3–5 mm. longi; folia infra saltem opposita aliquando in inflorescentibus subopposita vel alterna, palmatim in 3 (2–5) segmentis linearibus 5–20 mm. longis incisa, vel inferiora et superiora quandoque simplicia; flores non congesti, solitarii vel gemini in axillis foliorum superiorum; pedicelli graciles inaequales, 3–20 mm. longi; calyx 4–5 mm. longus, tubo 1 mm. longo, lobis linearibus 4 mm. longis, marginibus inferioribus ad sinus calloso-incrassatis infra sinus membranis parvis; corolla late infundibuliformis alba, longitudine rare 10 mm. excedens, tubo calycem aequante, vel subaequante, extus pubescente intus glabro, faucibus abrupte expansis 1.5–2 mm. longis, lobis obovatis 5 mm. longis, 2–3.5 mm. latis; stamina faucium in parte inferiora affixa, filamentis filiformibus glabris, 1.5 mm. longis, antheris luteis, 0.5 mm. longis e faucibus exsertis; ovarium 1 mm. altum, stylo 3–5 mm. longo ad medium in tres divisionibus linearibus inciso; fructus non visus; semina non visa.

Slender annual 3–12 cm. high, simple or with a few branches; internodes 5–50 mm. long with dense or sparse, weak short twisted hairs, becoming glabrate; cotyledons linear-spatulate, 3–5 mm. long; leaves opposite at least below, sometimes subopposite or alternate in the inflorescence, palmately cleft into 2 to 5 (normally 3) linear divisions, 5–20 mm. long, occasionally the lower and sometimes the upper simple; flowers solitary or in pairs in the upper leaf axils on slender unequal pedicels, showing little tendency toward congestion; pedicels 3–20 mm. long; calyx 4–5 mm. long, the tube 1 mm. long, the linear lobes 4 mm. long, lower margins of the lobes callous thickened toward and in the sinus, the sinus with a small membrane; corolla broadly funnelform, white, rarely exceeding 10 mm. in length, the tube equal or subequal to the calyx, pubescent externally, glabrous within; throat abruptly expanded, 1.5–2 mm. long, lobes obovate, 5 mm. long, 2–3.5 mm. wide; stamens inserted on the lower half of the throat, filaments threadlike, glabrous, 1.5 mm. long, anthers 0.5 mm. long, yellow, exserted from the throat; ovary 1 mm. high, style 3–5 mm. long, cleft to almost one-half its length into three linear divisions; fruit and seeds not seen.

Type. Southern end of Santa Maria plains, Baja California, Mexico, February 5, 1935, *Ira L. Wiggins 7557* (Dudley Herbarium, Stanford University, 263704; isotype, Herbarium of the University of California, 659206).

Linanthus Wigginsii is closely related to *L. Nuttallii* var. *floribundus* (Greene) McMinn from which it differs, however, in a number of significant characters. These differences may be best expressed by a key:

Plants perennial from a woody base, 1–5 dm. high; internodes stout; leaves 5 to 8 cleft, rarely subopposite; many-flowered, flowers sessile or short-pedicelled; calyx pubescent; corolla 12–20 mm. long, lobes 7–10 mm. long, spatulate to ovate; stamens included, filaments 1 mm. long, anthers 0.75 mm. long .... *L. Nuttallii* var. *floribundus*

Plants slender annuals, 3–12 cm. high; internodes slender; leaves 2 to 5 cleft, usually subopposite in the inflorescence; few-flowered; flowers short-pedicelled to long-pedicelled; calyx glabrous; corolla 8–10 mm. long, lobes 5 mm. long, obovate; stamens exserted, filaments 1.5 mm. long, anthers 0.5 mm. long .... *L. Wigginsii*

Linanthus Wigginsii seems definitely to establish a place for *L. Nuttallii* (Gray) Greene and its allies in the genus *Linanthus* rather than in the genus *Leptodactylon* where it has been placed by some authors. Its position in this latter genus has been maintained solely upon its perennial woody habit. The relationship between *L. Nuttallii* and *L. Wigginsii* is so close as to make generic separation impossible. Similarity between the two species may be noted in a tendency of the flowers to occur in pairs in the leaf axils, in the unequal pedicels of the paired flowers, in the shape, color and pubescence of the corolla, and in the very similar details of the calyx such as the thickening of the margins of the lobe and the nature of the membrane in the sinuses.

Department of Botany,
University of California, Berkeley,
February, 1942.

EBUROPHYTON HELLER: A VALID GENUS OF THE ORCHIDACEAE

Louis O. Williams

Eburophyton Austinae (Gray) Heller, Muhlenbergia 1: 49. 1904. *Chloraea Austinae* Gray, Proc. Am. Acad. 12: 83. 1876. *Cephalanthera oregana* Reichb. f., Linnaea 41: 53. 1876. *Cephalanthera Austinae* Heller, Cat. N. Am. Pl. ed. 2, p. 4. 1900. *Serapias Austinae* A. A. Eaton, Proc. Biol. Soc. Wash. 21: 66. 1908.

In 1876 Asa Gray described an orchid from California which he called *Chloraea Austinae*. *Chloraea* is a genus of orchids occurring in South America from the Falkland Islands north to Peru, with its greatest concentration of species in the Andes of Chile. *Chloraea* occurs mainly in open habitats and quite often in very hard, sterile soil. So far as I know no member of the genus is saprophytic. In the same year, 1876, H. G. Reichenbach described the same species, from a specimen collected by Nuttall, under the name of *Cephalanthera oregana*. *Cephalanthera* is a genus primarily of Europe and adjacent regions but one in which the species are not saprophytic. The third generic name was that applied by Heller in 1904, *Eburophyton*, a name designed to contain the single species in question. In 1908 A. A. Eaton placed the species in still a fourth genus as *Serapias Austinae*. Although the species has no special character to recommend its being placed in this genus it is here that it has been treated most often. Ames in "Enumeration of the Orchids of the United States and Canada" (1924), the most authoritative work yet published on the region covered, placed the species here.

Eburophyton Austinae is at once excluded from *Serapias* by its anther which is attached by a slender filament and is not solidly attached as in *Serapias*. From *Chloraea* it is distinguished by its saprophytic habit, by the lip being divided into an epichile and hypochile, with the hypochile gibbous at the base. From *Cephalanthera* the distinction is more difficult but the scarious nature of the leaves, saprophytic habit and geographical distribution would seem to indicate a separate genus.

Botanical Museum, Harvard University,
Cambridge, Massachusetts,

REVIEW

Standardized Plant Names. By Harlan P. Kelsey and William A. Dayton, prepared for the American Joint Committee on Horticultural Nomenclature. Second edition. Pp. xvi + 675. J. Horace McFarland Company, Harrisburg, Pennsylvania. 1942. $10.50.

As announced in the preface to the second edition "the purpose of 'Standardized Plant Names' is to bring intelligent order out of the chaos in names of plants and plant products existing the world over." We learn from the preface that the authors believe that the confusion in plant nomenclature is due to mistakes in identification and labeling and to disagreement in opinion, practice and judgment among botanists; we learn also that the general basis of the work of the committee appointed to bring "intelligent order" out of this chaos is "to agree arbitrarily upon some one name for each plant, by which name it can be designated for a definite term of years"; we learn to our chagrin that "a right label on the wrong plant or plant product may cause even more loss or disaster than the wrong label on the right plant or plant product" (page viii).

Throughout the preface there are presented certain rules whereby, as implied in the title, the names of plants are to be standardized. Although these rules are not definitely organized into a precise code of nomenclature, with a little patience one can collect and arrange them. The authors are aware of the rules adopted by the International Conference in London in 1930 but some of the rules promulgated by this conference from the standpoint of the present authors are inadmissable. They therefore accept what they like of these rules and reject what they do not like. Botanists have had similar experiences in bringing "intelligent order" out of chaos and were hampered by a similar group working from a nationalistic point of view, which if we mistake not, stemmed from the same habitat as this effort. It seems to the reviewer that since plants and plant products are a considerable item in international trade, their nomenclature is at once placed upon an international basis. Therefore, any attempt to standardize these names should result from international cooperation. This it would seem, is the intelligent basis for procedure and by not accepting it the authors violate the first point of their purpose.

It should be pointed out that the authors do not state specifically that their object is to develop a code of nomenclature but rather to "agree arbitrarily upon some one name for each plant." However, to standardize names implies that you have standards whereby this is to be accomplished. Moreover, if the rules mentioned in the preface are not to be used as a guide, why are they published in conjunction with plant names under a title that implies a code of standardization? The reader must assume that the authors intended that these rules should serve as a code or basis for the standardization of the nomenclature developed.

Several of the rules apply only to scientific names which are under the jurisdiction of the International Committee on Botanical Nomenclature and hence are not the concern of this or any other committee on horticultural names. Since horticultural interests are represented on the International Committee any use of scientific names at variance with the International Rules is unjustified and serves only to create confusion. Although it is always in order to recommend new rules to clarify plant nomenclature it is never in order for a small group to reject rules adopted through international cooperation.

These rules cannot correct mistakes in identification nor can they prevent disagreement in opinion, practice and judgment among botanists; these being the principal causes of confusion in the opinion of the authors. Rules of nomenclature should be aimed solely at matters which cause confusion in the names of plants. The consolidation of compound names adopted by the committee serves no useful purpose and more often than not, causes a name to violate the international code rule involving pronunciation and excessively long words. For example, try to pronounce "Gianthyssop", "Pussyears", "Sevenyearapple", "Globeamaranth", and "Holyghostflower." Consider "Browneye Babyblue-eyes Nemophila." We are not joking, this is the name the authors propose for *Nemophila atomaria* var. *discoidalis* (page 397). This rule as construed and practiced by these authors in many instances places the problem of the naming of plants upon a plane of ridiculousness never before achieved. We again call your attention to "Gianthyssop." To what language does it belong? It certainly is not English. These and hundreds of other proposed common names are a combination of good English words that by compounding have been translated into an atrocious form of pigeon English. When you write it, "Browneye Babyblue-eyes Nemophila" gets under the three-word limit by its beautiful eyelashes, but don't try to pronounce it as three words. After accepting certain rules the authors do not hesitate to practice methods of circumventing them. Although opposing the capitalization of specific and varietal names in the scientific nomenclature of plants, it is of interest to note that for common names no such concern is felt. Every word of a name is capitalized and in compounding words the capital letter is retained. Thus we find orthographical monstrosities such as "RockyMountain", "SanDiego", "EastIndies" and "SantaRosaIsland."

With respect to the application of the principle of priority to horticultural names certain difficulties need to be considered. Priority is a sound principle upon which to establish a stable nomenclature. It demands, however, that every name be documented with authority so that its position in the priority sequence can be established. Some of the names in this work that have been presented by societies such as the American Carnation Society and the Chrysanthemum Society are documented at least to originator but even in these the date is sometimes omitted. Unless there is maintained a specimen voucher or an adequate illustration we believe that it will be impossible at some future date to check against errors in identification and the misuse of names. The majority of the names used in the work give no evidence of supplying any basis whereby priority may be established if one should choose to apply it. To put horticultural names in a position to be standardized would require a major revolution in the practices of horticulturists with respect to giving and documenting the names of their plants. A system could be worked out by a qualified international committee for documenting names already in use and rules might be set up to which, in the future, authors would be required to conform. We are not concerned in nomenclature with the allocation of credit or honor for discovery or horticultural selection, we are concerned with responsibility for applying the correct name to a plant.

There are many more points that might be discussed in connection with this work and there is much that deserves credit. The chief criticism to be leveled against it is that the committee conceived of its problem as being one of giving plants names rather than one of proposing methods whereby the horticulturist could adjust his practices in naming plants so that standardization would be possible and nomenclature could be stabilized in as simple and dignified a manner as possible.—**Herbert L. Mason**, Department of Botany, University of California, Berkeley, California.

PROCEEDINGS OF THE CALIFORNIA BOTANICAL SOCIETY

January 22, 1942. Meeting, 103 Wheeler Hall, University of California, Berkeley, at 7:45 P.M. The retiring president, Professor E. B. Babcock, opened the meeting. Dr. Mildred E. Mathias requested, with regret, that the nominating committee withdraw her name from the list of nominations for 1942. The name of C. R. Quick was substituted by due process for nomination to the secretaryship. The following new officers were installed: Dr. Alva R. Davis, President; Dr. Palmer Stockwell, First Vice-President; Dr. Reed C. Rollins, Second Vice-President; Mr. Clarence R. Quick, Secretary; Dr. William M. Heisey, Treasurer. Dr. Davis, incoming president, introduced Dr. Reed C. Rollins, Instructor in Botany, Stanford University, who presented an interesting illustrated lecture on "The geographical distribution, speciation, and natural variation in Arabis and other Cruciferae."